

### Evolution of rock squirrels

The hoof-like form of the pollex in *Ratufa* indicates a preference for a hard stony substrate, but this squirrel is strictly arboreal, with arboreal digits. Perhaps the *Ratufini* paralleled the rock and tree hyraxes in form and function of the manus. Another possibility is that the pollex of *Ratufa* is adapted to standing on the main branches of trees, even more so than of *Sciurus*. The rock squirrel (*Spermophilus variegatus*) shows a moderately broad claw on the pollex. *Sciurotamias* also prefers rocky ground and possesses a fairly broad nail. Marmots often live in rocky habitat, and most of them possess a robust "nail" or hoof. The broad nail is apparently an adaptive, inconstant character in the *Sciuridae*.

### Evolution of tree squirrels and flying squirrels

Tree squirrels appeared as fossils in the Miocene (DAWSON, 1967; BLACK, 1963) and their record is only fair (see also MEIN, 1970). The arboreal pattern of the digits is seen in Asia, Africa, Europe and the Americas and is highly correlated to scansorial habits.

*Reithrosciurus* resembles *Sciurus* in general form, structure of the manus, and even of the baculum (see POCOCK, 1923, p. 214), but in its habits this squirrel has apparently returned to the ground (WALKER, 1964, p. 677). The fossil record for volant squirrels is also poor, although one is known from the Miocene (but see BLACK, 1963, p. 239). The volant squirrels possibly arose polyphyletically. PITERKA (1936) showed numerous arboreal-volant homologies, and BLACK (1963) suggested that some genera arose from *Sciurus* and other from *Callosciurus*. The structure of the manus in *Glaucomyss* and *Petaurista* is similar to that of *Sciurus* and other arboreal squirrels, except that *Petaurista* is advanced in loss of the pollex.

The *Petauristines* show amazing diversity in bacular form (POCOCK, 1923, p. 244–248) as well as in characters of the tail and flight membrane. *Eoglaucomyss* is most markedly divergent, though its baculum is possibly derived from the *Sciurus* pattern. The penis bone in *Petaurista* and *Hylopetes* though differing greatly could have developed from the pattern in *Sciurus*. The slender bone in *Glaucomyss* is not formed usually as figured by POCOCK, and resembles somewhat the bone in *Sciurus*.

### Summary and conclusions

Our study of the manus and consideration of other characters (tail, cheek pouches, penis, teeth) suggest that the *Marmotini*, as recognized by BLACK (1963) is as well differentiated as (or more so than) the *Petauristinae*. Although *Petauristines* are probably polyphyletic, with nevertheless a high degree of evolutionary homodynamy, the manus shows that their origin lies in arboreal squirrels probably taxonomically near *Sciurus*. The baculum in its diversity reflects nonetheless a *Sciurus* pattern. The holarctic ground squirrels (*Spermophilus*, *Cynomys*, and their close relatives) differ significantly from marmots in the form of the pollex. However, in anal glands and pattern of the digits of the manus the two groups show close relationship. *Ratufa* is distinctive in the *Sciurinae* in structure of the manus, and of the baculum (POCOCK, 1923). *Rhinosciurus* seems highly divergent from the arboreal and gliding squirrels in dental and cranial characters, and the foot shows little resemblance to them. *Petaurista*, *Rhinosciurus*, *Menetes*, *Myosciurus*, and *Nannosciurus* lack a pollex and are ruled out as ancestors of any of the other genera examined. *Nannosciurus* and *Menetes* resemble *Callosciurus* in bacular form (POCOCK, 1923, p. 220) and

apparently are descended from it or a close relative. New world chipmunks, *Tamiasciurus*, *Sciurotamias*, and *Rhinosciurus* neither resemble the arboreal forms nor the Marmotini in structure of the manus, and are somewhat intermediate in form of the manus. None of them should be arranged with the Sciurini in our opinion.

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#### Zusammenfassung

*Untersuchungen an der Hand von Sciuriden. I. Einige neue taxonomische Merkmale und ihre Bedeutung für die Klassifikation der Hörnchen*

Die Ausbildung der Vorderfußzehen wurde an einer großen Zahl von Sciuriden vergleichend untersucht und in ihrer taxonomischen Bedeutung erörtert. Bei grabenden Formen ist die 3., bei baumlebenden die 4. Zehe die längste. Zwischen beiden Gruppen vermitteln wenig spezialisierte, „artiodactyle“ Arten, bei denen 3. und 4. Finger gleich lang sind (*Tamias*, *Eutamias*, *Tamiasciurus*, *Sciurotamias* und *Rhinosciurus*). Unter den Marmotini nehmen amerikanische Arten durch den Besitz eines Nagels am Pollex eine Sonderstellung ein. Ein Daumen fehlt aber bei *Marmota marmota* wie auch bei manchen Baum- und Flughörnchen: *Petaurista*, *Rhinosciurus*, *Menetes*, *Myosciurus* und *Nannosciurus*. Im übrigen unterscheiden sich hinsichtlich der Finger die Marmotini von den anderen Sciurinae mehr als die Baumhörnchen von den Flughörnchen.

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# Biology of the rice rat (*Oryzomys palustris natator*) in a laboratory environment

## II. General skull morphology

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### Introduction

The rice rats of the genus *Oryzomys* form part of the muroid subfamily Cricetinae which includes approximately 60 groups currently accepted as having generic status. Taxonomic studies by ELLERMAN (1941) and RINKER (1954) have accepted 57 of these groups as being valid genera and there is enough evidence to warrant full generic status for the remaining groups.

Various taxonomists have endeavoured to bring order into the complex inter-relationships of the cricetine genera but, in spite of their efforts, confusion still exists and is regarded by RINKER (1954) as being partially due to the reliance placed by workers on what is an inadequate set of characters, and on the failure to make allowances for the phenomenon of convergent evolution which usually exhibits its most striking changes in the dentition.

The immense task of clarifying the inter-relationships within the Cricetinae has not moved far beyond the point reached by ELLERMAN (1941) apart from extensive work on the neotropical phyllotine group by HERSHKOVITZ (1944, 1955, 1960, 1962, 1966) and little can be added to his original comments although they are some 30 years old.

In the present survey, we are dealing with an inbred feral strain of rice-rat (*Oryzomys palustris natator*) whose introduction to a laboratory environment has already been reported (PARK, NOWOSIELSKI-SLEPOWRON 1972). The fact that ELLERMAN (1941) has shown cranial characteristics to be of no use in arranging a key to cover the Cricetinae since all are more or less generalized Muridae and there are few characteristics that cannot be duplicated in any of the large genera, means that we must approach the present interpretation of the skull with caution.

Basic description of *Oryzomys* characteristics — both general and skull — stems from the observations of MERRIAM (1901) and GOLDMAN (1918) although the original description was made by CHAPMAN (1893) in relation to *O. palustris natator*. One account of *Oryzomys palustris natator* skull morphology is included in MERRIAM's (1901) observations and is based on a small number of specimens. MERRIAM stated that „ . . . skull large and massive, elongated, flattened on top, with strongly projecting everted superciliary ridges, which greatly increase the breadth across the orbits posteriorly, zygomata moderately spreading; palatal slits large and open. Compared with *Oryzomys palustris palustris* the skull is much larger and heavier, with broadly expanded supraorbital ridges and much larger and more broadly open incisive foramina“.

It is obvious from these comments that the description of the rice rat skull morphology encompasses a wide range of variation and that, in the present study, we

are unable to make any comparisons between *O. palustris palustris* and *O. palustris natator*. At the present time, the Dundee rice rat colony can be envisaged as approaching the state of an inbred strain, thus variations which may have arisen cannot be compared with original wild stock until specimens are available from such stock. Our aim, therefore, is to present an account of the skull morphology of rats of the Dundee colony to allow some comparison to be made with the well-documented albino laboratory rat (*Rattus norvegicus*).

The future use of the rice rat as a laboratory animal depends partly on the establishing of a standard of existing morphology and partly on the sequence of the growth pattern without which no experimental procedures can be contemplated.

## Material and methods

*Rat Selection:* The material used for this study was obtained from a 1-month series of rice rats (*Oryzomys palustris natator*) ranging from 1 to 16 months inclusive. Over 100 rats were used of which there were approximately equal numbers of male and females. Animals derived from a 24-hour series covering birth to 30 days were also examined but were excluded from the present observations on the proviso that morphological standard should be made on mature animals before coming involved with developmental changes.

*Specimen Preparation:* The rats were killed by an overdose of ether, various body measurements were made for future work and the heads were removed and immediately placed in a solution of 2% calcium acetate/10% formalin at a pH of approximately 7. Maceration of the skulls was first attempted by means of 1% KOH and a 30–45 minute period in an ultrasonic cleaner bath (SPENCE, TONKINSON 1969), and then application of acetone to degrease, and bleaching by means of 5% of 100 vols. H<sub>2</sub>O<sub>2</sub>.

This particular method, however, had the drawback that, the skulls of many of the younger animals tended to separate along the suture lines while undergoing the ultrasonic waves. As a result, we returned to a longer but non-disrupting method in which the specimen was immersed in 1% KOH for approximately 3–5 days before attempting to remove the superficial soft tissue, de-cerebrating, degreasing and bleaching.

*Nomenclature:* The use of the latinized veterinary nomenclature of ELLENBERGER and BAUM (1926) would have been a natural first choice since it is specifically adapted to four-footed animals. With, however, a tendency to leave many of the Latin names out and replace these, in the anatomy world, with the B.N.A. nomenclature (JAMIESON 1916) the nomenclature used is that of the Birmingham Revision (B.R.) of the B.N.A. (The Basle Anatomical Nomenclature) terminology.

## Observations

Within a survey of the cranio-facial morphological characteristics of the rice rat lies not only the topology of the skull as a whole, but also each bone its relationship with adjacent bones.

The rice rat skull consists of the same basic bone elements as are found in any rodent and can be tabulated as shown on page 105.

To introduce the general characteristics of rice rat skull morphology, standard views of the adult rice rat skulls have been drawn in detail. Examination of both male and female skulls within the sample aged 1–16 months revealed no significant sex difference apart from that of size, therefore the morphology has been presented in drawings of the adult male (Figs. 1, 2, 3, 4, 5, 6, 7).

## Discussion

The present intention is not to cover all the aspects of the bones and their inter-relationships but rather to introduce the general characteristics of rice rat skull topology



| Birmingham Revision<br>of B.N.A. | ELLENBERGER<br>and BAUM | Birmingham Revision<br>of B.N.A.                               | ELLENBERGER<br>and BAUM  |
|----------------------------------|-------------------------|--|--------------------------|
| 2 nasals                         | os nasale               | 2 parietals  | os parietale             |
| 2 premaxillaries                 | os incisivum            | 1 occipital  | os occipitale            |
| 2 maxillaries                    | os maxilla              | 1 interparietal  | os interparietale        |
| 2 zygomas                        | os zygomaticum          | 2 squamosals   | os squamosum             |
| 2 palatines                      | os palatinum            | 2 periotic capsules  | os perioticum            |
| 1 vomer                          | os vomer                | 2 tympanic bullae  | os tympanicum            |
| 2 lacrimals                      | os lacrimale            | 6 auditory ossicles<br>(2-malleus, 2-incus,<br>2-stapes)       | malleus, incus<br>stapes |
| 1 ethmoid                        | os ethmoidale           | 4 conchae<br>(turbinates)<br>dorsal concha,<br>ventral concha) | conchae nasalis          |
| 2 frontals                       | os frontale             | 1 hyoid  | os hyoideum              |
| 1 basisphenoid                   | os sphenoidale          | 2 mandibles  | os mandibula             |
| 1 presphenoid                    | os sphenoidale orale    |  |                          |

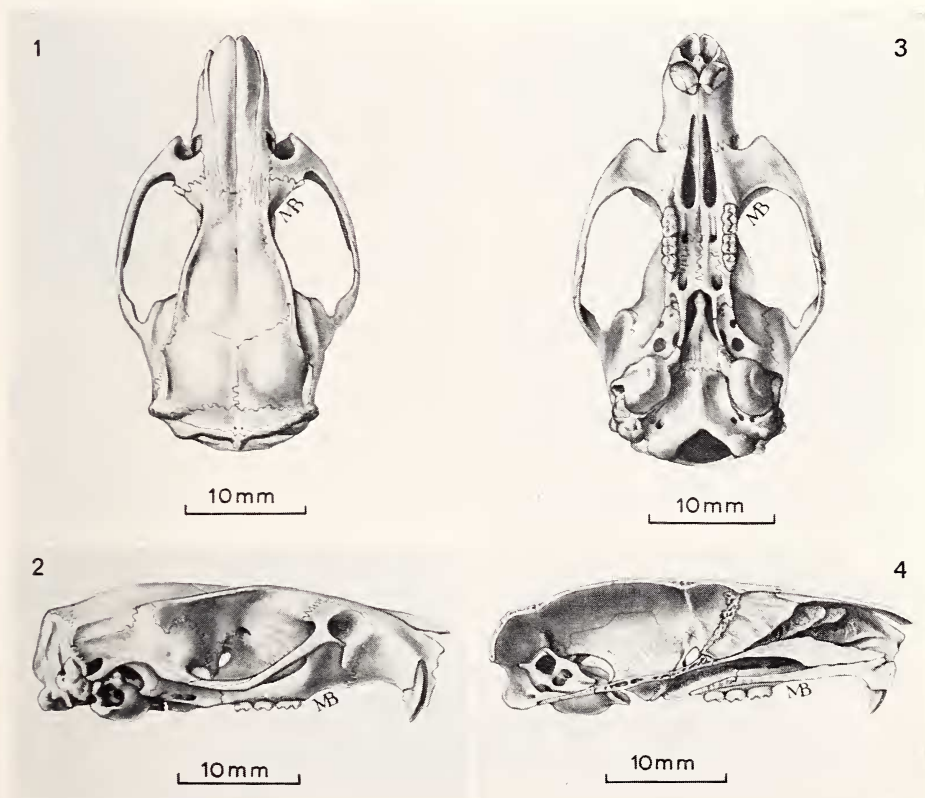


Fig. 1. Skull morphology of adult rat (*Oryzomys palustris natator*) dorsal aspect. — Fig. 2. Lateral aspect. — Fig. 3. Ventral (basal) aspect. — Fig. 4. Lateral aspect of a section taken through the median sagittal plane

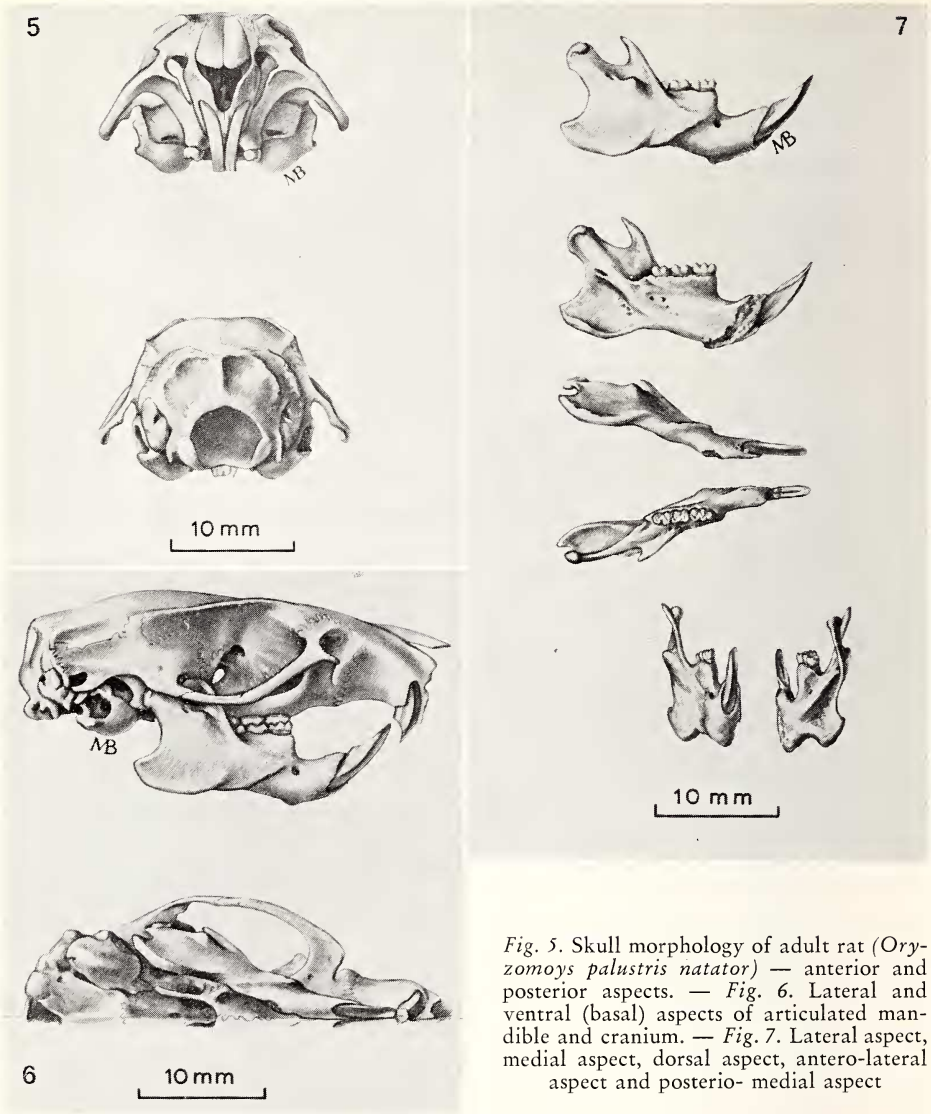


Fig. 5. Skull morphology of adult rat (*Oryzomys palustris natator*) — anterior and posterior aspects. — Fig. 6. Lateral and ventral (basal) aspects of articulated mandible and cranium. — Fig. 7. Lateral aspect, medial aspect, dorsal aspect, antero-lateral aspect and postero-medial aspect

and a number of simple comparisons with the albino laboratory rat (*Rattus norvegicus*). It is obvious that, except for its basic taxonomy, the rice rat has not been subjected to any extensive study apart from a comparative study of the hyoid apparatus (SPRAGUE 1941) and the much older descriptions of CHAPMAN (1893), MERRIAM (1901) and GOLDMAN (1918). As far as studies of the rice rat in a laboratory environment extend, apart from behavioral analysis — which does not concern us here — a little descriptive work has been undertaken by GUPTA and SHAW (1956) on tooth morphology and eruption, observations on aspects of genetics and development of fused molars (GRIFFITHS, SHAW 1961; SHAW, GRIFFITHS, OSTERHULTZ 1963; SOFAER, SHAW 1971), and on the presence of periodontal disease (GUPTA, SHAW 1955, 1956; GUPTA, AUSKAPS, SHAW 1957; SHAW, GRIFFITHS, AUSKAPS 1961; SHAW 1965 a and b, SHAW 1966; SHAW, KRUMINS 1966; SHAW, DICK 1966; DICK, SHAW 1966; DICK, SHAW,

SOCRANSKY 1968). Some work on the effect of protein-deficient diets on the bones of different genera of rat, including the rice rat, was reported by PACK and LUCAS (1971). The rice rats used in this work came from the daughter colony originally established by rats sent from the Dundee colony.

The general characteristics of the rice rat skull are more clearly shown in the drawings than in lengthy descriptions. On examination the skull is found to be fairly large, with flattening occurring over the dorsal region. The superciliary (supraorbital) ridges are definitely everted and projecting resulting in an increase in the breadth of the skull across the orbits posteriorly. In a similar way, the zygomatic complex shows a wide spreading while the anterior palatal foramina are long — reaching back to a line drawn at right angles to the foramina and joining the right and left first maxillary molar teeth. The frontal bones taper into a narrow point posteriorly in the median line between the parietal bones. The interparietal bone is small and its anterior border forms a straight line while a poorly defined median angle occurs posteriorly. The mandible has a broad angle and the coronoid process reaches above the level of the condylar process. It is proposed, at a later date, to publish a more detailed account of the individual bones forming the rice rat skull and of the dentition.

When attempting the description of the morphology of a particular rodent skull about which there is only a limited amount of known data, it is natural to try and attain perspective by using some baseline whereby comparisons can be demonstrated. To allow such comparison to be made, the well-documented albino laboratory rat (*Rattus norvegicus*) proved to be an excellent foil in previous work (PARK 1972) and has been used in the present work. When the skulls of these two species are compared several differences are revealed besides the more obvious one of size. The following list can only be regarded as a tentative one and used as a rough guide until further information on the variations are established.

1. The antero-posterior alignment of the maxillary and mandibular tooth rows is almost parallel in the rice rat whereas in the albino laboratory rat, greater curvature and a slight divergence posteriorly is shown.
2. The angulation of the mandibular molar teeth towards the median sagittal plane is more pronounced in the albino laboratory rat.
3. The anterior palatine foramina of the rice rat are much longer than those of the albino laboratory rat.
4. From both dorsal and ventral aspects, the squamosal bones of the rice rat as they curve laterally and anteriorly to meet the zygomatics, have small but definite notches medial to the zygomatic process.
5. The frontal bones of the rice rat taper into a narrow point posteriorly, in the median line between the parietal bones — along the coronal suture line. This particular suture junction is relatively straight in the albino laboratory rat.
6. The interparietal bone is very narrow in the rice rat, compared with the albino laboratory rat, and forms a relatively straight line along its anterior border. In the albino laboratory rat, the anterior border ends in a small notch or wedge.
7. In the mandible, the coronoid process is more vertically orientated in the rice rat and also more pointed. As a result of this the mandibular notch is deeper and wider than in the albino laboratory rat.
8. The angular process of the mandible of the rice rat is shorter and rounder, and does not extend so far posteriorly beyond the condylar process as it does in the albino laboratory rat.

#### Summary

General morphological characteristics of the skull of the recently introduced rice rat have been described following some 15 generations under laboratory conditions. Approximately